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XII.—*On the Homology of the Organs of the Tunicata and the Polyzoa.** By GEORGE JAMES ALLMAN, M. D., F. R. C. S. I., M. R. I. A., Professor of Botany in the University of Dublin.

Read January 26, 1852.

THOUGH the close affinity between the *Tunicata* and the *Polyzoa* has been generally acknowledged, yet the full extent to which the organization of the one is represented by that of the other does not appear to have been hitherto recognised by the zoologist. I propose in the present communication to point out some apparently unnoticed instances of homological identity, while I shall endeavour to show that almost every modification of form in the organization of the one is, by the easiest transition, convertible into a corresponding form in the other; that they are both, therefore, constructed on precisely the same type, and must constitute one and the same great natural group.

In order to render this subject intelligible, it will be necessary in the first place to fix the terms indicative of the various aspects of the *Tunicata* and the *Polyzoa*, terms which are so vaguely used by different authors as to give rise to great confusion in description. In the determination of the *anterior* and *posterior* aspects, there would seem to be no difficulty, as the former must manifestly be assumed as that to which the mouth is directed, while the posterior will then of course be the aspect directly opposed to this. The determination of the *dorsal*, or *superior*, and of the *ventral*, or *inferior* aspects, is not so easy. I believe, however, that the *cephalic ganglion*, or its homologue, must be here our true guide, and that its position will always correspond with the dorsal, or superior aspect of the animal, to which the ventral will then consequently be diametrically opposed. MR. HUXLEY, in his admirable memoir on *Salpa* and

* *Polyzoa* THOMPSON, synonymous with *Bryozoa* EHRENBURG. THOMPSON's name has priority of date over that of EHRENBURG, and should, therefore, in justice to its founder, and in obedience to the laws of Natural History nomenclature, be adopted.

Pyrosoma, assumes the *heart* as indicating the dorsal aspect of the *Tunicata* ;* the cephalic ganglion, however, in those inferior members of the animal kingdom in which the dorsal and ventral aspects are already indicated by other characters, is invariably placed on the dorsal side of the alimentary canal, and though it be admitted that the almost universal position of the heart among invertebrate animals is also dorsal ; yet where, as in the *Tunicata*, we find the ganglion and heart placed on opposite sides, the superior importance of the ganglion will, I think, justify us in assuming its position as the *constant* one, and concluding that it is the heart therefore and not the ganglion that has changed place. The only apparent difficulty in assuming the ganglion as the index of the back results from its not being always obvious that the nervous mass before us is homologous with a true cephalic, or supra-oesophageal ganglion ; there will, however, I think, always be found marks sufficient to decide this point ; we shall subsequently see that the ganglion, both in the *Tunicata* and the *Polyzoa*, undoubtedly contains a supra-oesophageal element, which from its pre-eminent importance will determine the

FIG. 1.

FIG. 2.

FIG. 1. Diagrammatic view of *Clarelina*.
 FIG. 2. Diagrammatic transverse section of *Clarelina*.†
a, external tunic ; *b*, middle tunic ;
c, internal tunic ; *d*, *d*, *d*, sinus system ;
e, respiratory orifice ; *f*, cloacal orifice ;
g, *g*, transverse respiratory bars ; *h*, *h*, longitudinal respiratory bars ; *i*, branchial sinus ;
k, *k*, proper membrane of respiratory sac ;
l, languets ; *m*, mouth ; *n*, oesophagus ;
o, stomach ; *p*, intestine ; *q*, anus ; *r*, cloaca ; *s*, tentacula ; *t*, muscular fibres in middle tunic ; *u*, heart ; *v*, nervous ganglion ; *w*, gemma.

* "Observations upon the Anatomy and Physiology of *Salpa* and *Pyrosoma*, together with Remarks on *Doliolum* and *Appendicularia*." By Thomas Henry Huxley. Phil. Trans., 1851.

† In all the figures accompanying this paper, the same letters are used with the homologous organs.

dorsal position of the ganglionic mass, even though the latter should also perform functions usually devolving on ganglia situated below the alimentary canal.

1. Respiratory System.

tem.—As it is in the respiratory organs of the two groups that the leading peculiarities of their structure are to be found, our attention must be first directed to this portion of the organization, with the view of determining how far the respiratory apparatus in the one has its homologue in the other. Now two distinct notions have prevailed on this point, some zoologists* maintaining that the res-

FIG. 3.

FIG. 4.

FIG. 3. Diagrammatic view of a *hippocrepian Polyzoa* (retracted). FIG. 4. Diagrammatic transverse section of a *hippocrepian Polyzoa*.

a, ectocyst; *b*, endocyst; *c*, tentacular sheath; *d*, *d*, *d*, perigastric space; *f* + *e*, external orifice of cell; *g*, *g*, tentacula; *i*, lophophore; *k*, *k*, caliciform membrane; *l*, oral valve-like organ; *m*, mouth; *n*, oesophagus; *o*, stomach; *p*, intestine; *q*, anus; *r*, cavity of tentacular sheath; *t*, muscular fibres in endocyst; *v*, nervous ganglion; *w*, gemma.

piratory sac of the Ascidian has its representative in the pharynx of the Polyzoa, and that the rudimental tentacula at the orifice of this sac are homologous with the tentacula of the Polyzoa; while others† assert, that the branchial sac of the *Ascidiae* is homologous with the tentacular crown of the Polyzoa, the longitudinal bars of the sac corresponding to the tentacula of the Polyzoa, and the transverse bars becoming extinct. Now, neither of these views appears to me to represent the exact truth, for, while I conceive that the tentacular crown of the Polyzoa has undoubtedly its true homologue in the respi-

* See Dr. A. FARRE, "Observations on the Minute Structure of some of the higher Forms of Polypi." Phil. Trans. 1837.

† See VAN BENEDEK. "Sur les Ascidies Simples." Mem. de l'Acad. Roy de Belgique, Tome xx. 1847.

ratory sac of the *Ascidiae*, I believe that it is to the *transverse*, and not to the longitudinal bars of this sac that the tentacula of the Polyzoa are homologous ; and this is a very important distinction, the non-recognition of which has rendered all previous attempts at comparison between the tentacular crown of the *Polyzoa* and the respiratory sac of the *Ascidiae* untenable.

On this subject much light is thrown by the *hippocrepian Polyzoa*, or those fresh-water genera which, like *Plumatella*, have their tentacula arranged on a crescentic "lophophore;"* and we shall best perceive the relations in question by comparing an ascidian Tunicate with one of these *Polyzoa*, a *Clavelina* (Figs. 1 and 2), for example, with a *Plumatella* (Figs. 3 and 4). In *Clavelina*, the great "branchial sinus" of MILNE-EDWARDS,† from each side of which the transverse bars or vessels of the respiratory sac are given off, will correspond to the elongated lophophore in *Plumatella*, and the richly ciliated transverse bars to the ciliated tentacula, while the delicate membranous sac, to the interior of which the respiratory bars are adherent, and which MILNE-EDWARDS has shown to be perforated in the intervals of these bars by the "respiratory stigmata," will have its homologue in the calyx-like membrane adherent to the base of the tentacular plume in *Fredericella* and the hippocrepian *Polyzoa*. This correspondence will be rendered more obvious by imagining the branchial sinus to be rotated round its oral extremity in a vertical plane through an angle of 90°, towards the superior or anal side of the Tunicate ; its position from longitudinal will thus be changed to transverse, while the transverse bars will become longitudinal, and the branchial sinus and its bars will then have the same direction as the exserted lophophore and tentacula of *Plumatella* ; while it is interesting to observe that, during the retracted state of the Polyzoan, the lophophore assumes the normal direction of the branchial sinus in the Tunicate.

That the tentacula of the *Polyzoa* are not homologous with the unciliated

* In a Report on the Fresh-Water *Polyzoa*, read before the Edinburgh Meeting of the British Association for 1850, I found that our increased knowledge of the structure of the *Polyzoa* rendered it necessary to make some change in the terminology hitherto employed in their description ; and the terms used in that Report are also adopted in the present memoir. The *Polyptide* is the retractile portion of the Polyzoan as distinguished from its cell ; the *Ectocyst* is the external tunic of the cell ; the *Endocyst* is the internal tunic ; the *Lophophore* is the kind of disc or stage which surrounds the mouth and bears the tentacula.

† See M. MILNE-EDWARDS's beautiful memoir, "Sur les Ascidies Composées."

rudimentary tentacula at the entrance of the respiratory sac in the *Ascidiae* is also apparent, not only from the difference of structure, but from the fact, that while the tentacula of the *Polyzoa* are in immediate relation with the digestive tube, those of the *Ascidiae* are evidently mere appendages of the internal tunic. It is true, that in accordance with this view, we can find no homologue in the *Polyzoa* for the tentacula of the *Ascidiae*; we must therefore conclude, that these organs have absolutely died out in the *Polyzoa*, a circumstance for which we have been already prepared by their disappearance in *Salpa* and other Tunicates.

In connexion with the tentacular crown, there is another part of the organization of the *Polyzoa* for which we have still to find an equivalent, and which, without comparison with the *Tunicata*, would remain inexplicable, namely, the curious valve-like organ which overhangs the mouth in *Fredericella* and the hippocrepian *Polyzoa*. Now this is plainly homologous with the tongue-like bodies, the "languets" of MILNE-EDWARDS, which are attached along the branchial sinus in *Clavelina* and certain other Tunicates, and thence project into the interior of the branchial sac, and which in *Salpa* are represented by a single one. The languet in *Salpa* is connected with a peculiar ciliated cavity lying immediately at its base, and which seems also to have its representative in the excavation of the lophophore at the base of the oral appendage in *Plumatella* and the allied forms; and through which the cavity of this appendage appears to communicate with the perigastric space. Further observation will, in all probability, prove that the interior of the languets in the *Tunicata* communicate in these with the great "sinus system,"* which is equivalent with the perigastric space of the *Polyzoa*. MILNE-EDWARDS believes the languets in *Clavelina* to exhibit a kind of erection, a phenomenon which would suggest as its explanation such a communication as that here supposed, and which, at all events, renders still more striking the resemblance between the languets of the *Tunicata* and the oral appendage of the *Polyzoa*, an organ which seems to present an analogous phenomenon. In both groups the bodies in question would seem to be organs of special sense, probably of taste.

* This name has been given by HUXLEY to the whole of the space included between the internal and middle tunics in the *Tunicata*, and through which the blood, uninclosed in proper vessels, vaguely circulates. See HUXLEY, loc. cit.

We now need only a few unimportant modifications in order to complete the resemblance between the branchial sac of *Clavelina* and the tentacular crown of *Plumatella*; we have only to imagine the oral extremity of the branchial sinus to be prolonged with its bars for a short distance downwards, so as to surround the mouth, the transverse bars to become free at their extremities, where, opposite to the branchial sinus, they communicate with the "thoracic sinus," the longitudinal bars to be suppressed, and the "languets" to be reduced to *one* situated in the immediate vicinity of the mouth; a series of changes involving no essential modification of structure; and we shall then have an organ only wanting in a deep crescentic depression of the distal extremity of the branchial sinus, to resemble, even in minute details, the tentacular crown of *Plumatella*.

Now nearly all the changes which we have thus hypothetically supposed to take place in *Clavelina*, in order to convert its branchial sac into the tentacular crown of *Plumatella*, do actually occur in other genera of *Tunicata*, some in one, and some in another. The predominant importance of the transverse over the longitudinal bars of the branchial apparatus in the *Tunicata* is sufficiently manifest; in most cases they are larger and more evident than the longitudinal; in *Pyrosoma*, as appears from Mr. HUXLEY's account of this genus,* they are not only the better developed, but they alone carry cilia; the transverse bars, moreover, are constant in all the genera, while the longitudinal actually disappear in *Salpa* and in *Doliolum*, unless, indeed, we adopt the ingenious view of Mr. HUXLEY, who supposes that the lower division ("Epipharyngeal Band" of HUXLEY) of the gill in *Doliolum* is homologous with the longitudinal bars in *Pyrosoma* and other tunicates; an opinion, however, which is surely opposed by the fact, that in two species of *Salpa* examined by SAVIGNY, this naturalist has pointed out the existence of a small inferior gill, maintained by Mr. HUXLEY to be the homologue of the inferior division of the gill in *Doliolum*; and yet the superior or constant gill in one of these *Salpæ* shows at the same time traces of longitudinal bars as in *Pyrosoma*. In *Doliolum*, as it would appear from Mr. HUXLEY's short but interesting account, the superior and inferior divisions of the gill are directly continuous with one another behind; indeed they are evidently one and the same organ carried across the thoracic chamber

* Loc. cit.

(Fig. 5); the gill in *Doliolum* then plainly consists of a great branchial sinus, carrying its respiratory bars on each side as in *Clavelina*, but differing from the disposition of parts in the latter genus by having its posterior extremity prolonged downwards till it reaches the inferior wall of the thoracic chamber, along which it then runs forwards parallel to the superior portion. The mouth perforates this inferior prolongation of the sinus, and thus becomes related to the sinus and its bars exactly as the mouth in the *Polyzoa* is to the lophophore and tentacula in these. SAVIGNY informs us, that the mouth opens between the inferior and superior gill in the *Salpæ* examined by him; but it is not easy to determine from his description whether these portions are directly continuous, as in *Doliolum*. In *Doliolum*, moreover, the remote extremities of the branchial bars of one side are quite separate from those of the other, and thus present the open condition which characterizes the tentacular crown in the *Polyzoa*, so that the gill of *Doliolum* constitutes the exact link by which the branchial sac of the *Ascidiae* passes immediately into the tentacular crown of the *Polyzoa*. In *Pyrosoma* we have also an approach to the open condition of the tentacular crown, for the inferior extremities of the transverse bars of one side are separated from those of the other by a considerable space, and, according to LESIEUR, even become free for some distance from their extremities in the species which he describes.

The structure and connexions, then, of the ascidian tentacula, together with the modifications actually experienced by the longitudinal and transverse bars in the different forms of *Tunicata*, and the fact that the tentacular crown in the hippocrepian *Polyzoa* will admit of a satisfactory explanation in accordance alone with the views here taken, afford evidence that the homologues of

FIG. 5.

FIG. 5. Ideal longitudinal section of *Doliolum*.

a + b, external and middle tunic united; *c*, internal tunic; *d, d*, sinus system; *e*, respiratory orifice; *f*, cloacal orifice; *g*, respiratory bars; *i, i*, branchial sinus; *m*, mouth; *n*, cesophagus; *o*, stomach; *p*, intestine; *q*, anus; *r*, cloaca; *v*, nervous ganglion.

the tentacula in the *Polyzoa* are neither the rudimentary tentacula at the entrance of the branchial sac of the *Ascidiae*, nor the longitudinal bars of this sac, as maintained by those naturalists who have yet recognised in the branchial sac of the *Ascidiae* an organ homologous with the tentacular crown of the *Polyzoa*; but that their true equivalents must be sought for in the transverse bars, and this is further borne out by the observation of the ascidian embryo in which the longitudinal bars would seem to make their appearance subsequently to the transverse ones; the respiratory sac thus passing in the course of its development through a stage more nearly corresponding to the simpler condition which we meet with in the respiratory crown of the *Polyzoa*.

In *Salpa* the languets are reduced to a single one, that, however, which remains in this genus is not, as we might be led to expect from the comparison we have made between these organs and the oral appendage of *Plumatella*, the languet nearest the mouth, but on the contrary (if we may judge from its position), the most remote from this part of the animal. It is, however, particularly worthy of attention, that both the existing languet of *Salpa* and the oral appendage of *Fredericella*, and the hippocrepian *Polyzoa*, are quite similarly related to the great nervous ganglion. This ganglion we shall presently see to be homologous in the *Tunicata* and *Polyzoa*, and it is manifestly it, and not the mouth, that determines the place of the persistent languet.

However interesting the hippocrepian *Polyzoa* may be in directly indicating the relations here dwelt on, the infundibulate genera present no difficulty, for they exhibit, after all, but an unimportant modification of the former, and are connected to them by a series of intermediate forms. The arms of the lophophore in *Plumatella* have only to become obsolete in order to transform this genus into a *Fredericella*, in which, however, the lophophore still retains a bilateral figure, which is rendered yet more decided by the presence of the oral valve-like organ. In *Laguncula* VAN BEN., the oral appendage has disappeared, but the lophophore still presents a slight bilaterality. Finally, in the fresh-water genus, *Paludicella*, and most of the marine genera, not only has the oral appendage disappeared, but all trace of bilaterality has now vanished from the lophophore.

2. *Dermal System*.—M. MILNE-EDWARDS has proved by the anatomy of *Clavelina*, that there exist in this genus, and probably in all *Tunicata*, three distinct

envelopes, which, however, may be variously united with one another in the different genera.* Now all these have their homologues in the *Polyzoa*; the external sac or test of the *Tunicata* corresponds to the external investment, or ectocyst, of the *Polyzoa*; the middle sac, or mantle, of the *Tunicata*, to the internal investment, or endocyst, of the *Polyzoa*; and the internal tunic of the *Tunicata*, which surrounds the branchial sac, and forms the "thoracic chamber" of MILNE-EDWARDS (and which is divided into two portions, one inferior, containing the proper branchial sac, and the other superior, constituting the cloacal chamber), will be equivalent with the tentacular sheath of the *Polyzoa*. The homology of the two outer tunics of the *Tunicata* with the ectocyst and endocyst of the *Polyzoa* is obvious, and need not here be further dwelt upon; but the homology of the third or innermost tunic of the *Tunicata* with the tentacular sheath of the *Polyzoa* is very important, and will require to be considered more in detail. If we examine this tunic in *Clavelina*, we shall find that it is continuous with the mantle at the respiratory and cloacal orifices, and becomes attached to the alimentary canal, just behind the mouth and anus. It thus holds to the surrounding parts in the *Tunicata* exactly the same relation that the tentacular sheath or inverted tunic in the *Polyzoa* does to the corresponding parts of these during the retracted state of the animal. In the *Polyzoa* there is, properly speaking, but one external orifice, namely, that through which the tentacular crown is projected and retracted; but this is equivalent to the respiratory and cloacal orifices of the *Tunicata* united, and the point where the rectum opens externally in the *Polyzoa* is not, therefore, as supposed by VAN BENEDEK and others, the homologue of the cloacal orifice in the *Tunicata*, with the cloacal chamber itself become extinct,—a view which evidently originated in the too exclusive contemplation of the Polyzoan in its exserted state,—but rather corresponds to the point where the rectum penetrates the internal tunic in the *Tunicata*, and the cloaca in the latter will then be represented by the superior or dorsal portion of the space between the tentacular crown and sheath in the *Polyzoa*, this space becoming obliterated in the exserted state of the polypide.†

* See HUXLEY, loc. cit.

† To the normal structure both of the *Tunicata* and the *Polyzoa*, *Appendicularia* presents a remarkable exception. In this singular little Tunicate, as described by HUXLEY, the branchiæ are reduced to a mere rudiment, and while the thoracic chamber formed by the internal tunic is largely

3. *Digestive System.*—The form, structure, and peculiar course of the alimentary canal in the *Tunicata*, closely resembles what we find in the *Polyzoa*. This canal in the *Polyzoa* consists of three distinct portions: œsophagus, stomach, and intestine; the œsophagus communicates with the stomach by a well-defined cardiac orifice, and the cardiac extremity of the stomach frequently presents a cylindrical elongation, with the œsophagus opening into its anterior end; the stomach is separated from the intestine by a well-marked pylorus. The alimentary canal in the *Tunicata* is also divided into œsophagus, stomach, and intestine; in some instances these divisions are obscurely marked, but in others they are as well defined as in the *Polyzoa*. Now if, in accordance with the views attempted to be established in the present memoir, we consider the branchial sac of the Ascidian as the homologue of the tentacular crown of the Polyzoan, we shall have the three regions of the alimentary canal of the one exactly homologous respectively with the three regions in the other. If, on the contrary, the branchial sac of the Ascidian be homologous with the first region—the pharynx or œsophagus—of the alimentary canal of the Polyzoan, then, in order to find a homologue in the Polyzoan for that portion of the canal which intervenes between the branchial sac and the stomach in the Ascidian, and which is without doubt a true œsophagus, differing altogether in structure from the stomach, wherever in the *Tunicata* the alimentary canal acquires its proper development, we must take the cardiac prolongation of the stomach in the *Polyzoa* for an œsophagus, a view not borne out either by its structure or its functions; for independently of the fact that it is not always present, this prolongation obviously belongs to the proper stomach, having, it is true, special muscles sometimes developed in it, so as to give it the structure and office of a gizzard;* but more frequently being a simple prolongation of the gastric cavity, in no respect differing from the remainder of this cavity either in structure or func-

developed, the intestine does not open into it, but passes forwards and downwards to perforate the middle and external tunics, and thus open directly outwards. There is consequently here no cloaca. *Appendicularia* at a first glance appears to afford the connecting link between the *Tunicata* and the *Polyzoa*; but a little consideration will show that the most important point by which it differs from the normal *Tunicata*, namely, the absence of a cloaca, is that which also separates it at the greatest distance from the *Polyzoa*.

* See "Report on Fresh-water Polyzoa." Rep. Brit. Assoc., 1850, p. 310.

tion. In both the *Tunicata* and the *Polyzoa* the intestine is invariably bent on the first portion of the alimentary tube as it passes forward to the anal outlet; but there is a curious difference between the two groups in this respect, namely, that while in the *Tunicata* the first bend of the intestine, as noticed by Mr. HUXLEY, is always towards the lower side, or that opposite to the ganglion, its whole course in the *Polyzoa* is as invariably towards the upper, or ganglionic side, a difference, however, in no degree invalidating the homological identity of the parts. The structure of the walls of the alimentary canal in the *Tunicata* reminds us strongly of that in the *Polyzoa*. In some *Tunicata* there is a well-developed liver; in others, however, this organ is entirely absent, or only represented by a peculiar coloured layer on the interior of the walls of the alimentary canal, exactly as in the *Polyzoa*.

4. *Circulatory System*.—The circulatory system of the *Tunicata* admits of a very interesting comparison with that of the *Polyzoa*. The degraded condition of the vascular system in the former, where the heart scarcely advanced beyond the embryonic condition, is alternately branchial and systemic; and the undefined or extra-vascular circulation in the whole of the abdominal region conduct us at once to the complete absence of the heart in the *Polyzoa*, where the circulation—altogether extra-vascular, except so far as the tubular tentacula and lophophore represent a vascular system—is effected by the propulsive action of vibratile cilia. The condition of the circulatory system in the *Polyzoa* has already been quite anticipated in the curious Tunicate genus *Pelonaia*,* where the heart itself has disappeared. The great “sinus system” of the *Tunicata*, filled with the vaguely circulating blood, has its exact homologue in the perigastric space of the *Polyzoa*, occupying, like the latter, the interval between the middle and internal tunics.

5. *Muscular System*.—The muscles on which devolves the office of the retraction of the polypide in the *Polyzoa* are of course absent in the *Tunicata*, but notwithstanding this, we have some interesting points of correspondence between the muscles of the two groups. In the middle tunic or mantle of the *Ascidiae* there is, as is well-known, a large development of muscular tissue in the form of circular and longitudinal fibres, which give to this tunic its cha-

* See FORBES and GOODSR in Edinburgh New Phil. Jour., vol. xxxii. p. 29.

racteristic contractility. Now these muscles are exactly represented by equivalent fibres which are developed in the homologous tunic or endocyst of the *Polyzoa*, and constitute the "parietal muscles" of these animals. The circular bands of *Salpa* and *Doliolum* appear to be developed in the *internal* tunic, and have their representatives in the sphincters occurring in the inverted tunic of the *Polyzoa*. Striated muscular fibre exists in many, if not in all the *Polyzoa*, and a similar condition of this tissue has been detected by ESCHRICHT and HUXLEY in *Salpa*.

6. *Nervous System.*—Between the great nervous ganglion in the *Tunicata* and the *Polyzoa* there is apparently a marked difference in position, this ganglion in the *Tunicata* being placed between the respiratory and cloacal orifice, while in the *Polyzoa* it is situated on the œsophagus near its oral extremity, and this difference might at first lead to the belief, that the homological identity which we have witnessed between the other organs of the two groups fails to show itself in the nervous system; still, however, it can be rendered evident, that no exception is here offered to the unity of plan already demonstrated, and that the two ganglia are strictly homologous. The ganglion is manifestly identical in function in the two groups, for in each we have nerves passing off from it both to the respiratory apparatus and to the œsophagus and region of the mouth, a distribution in which it corresponds with that of both the branchial and cephalic ganglia of the higher *Mollusca*, whose offices it thus seems to combine.

In several of the *Tunicata*, a well-defined otolithic capsule has been discovered in connexion with the ganglion; and Mr. HUXLEY has suggested to me that this ganglion ought therefore to be considered as homologous with the pedal ganglion of the Lamellibranchiate *Mollusca*, since in these the otolithic capsule is always found in connexion with the pedal ganglion. To this view, however, several objections appear to me to present themselves; the ganglion of the *Tunicata* and of the *Polyzoa* has functions devolving on it which we never see performed by the pedal ganglion of the *Lamellibranchiata*; the development of the pedal ganglion, moreover, bears a constant relation to that of the foot, and though the obliteration of the foot does not necessarily bring with it the absence of the ganglion—as in *Teredo*, for example, where the researches of QUATREFAGES have shown the existence of a pair of minute ganglia, manifestly re-

presenting the pedal ganglia of those *Lamellibranchiata*, in which the foot is not suppressed,—yet the pedal ganglion presents us under such circumstances with its lowest condition of development, and analogy will not permit us to suppose that in the absolutely footless Tunicate or Polyzoon this ganglion acquires its maximum, and even becomes here the only nervous centre present. It would, indeed, seem as if the solitary nervous centre of the *Tunicata* and *Polyzoa* combined the functions of the several separate centres of the *Lamellibranchiata*, while the superior importance of the cephalic element determines its supra-oesophageal position.

If we now carefully consider the difference of position between the two ganglia, we shall find that this is, after all, unimportant ; in the *Tunicata*, while the ganglion is always placed between the two external orifices, it is at the same time situated in the interval between the internal and middle tunic, and is consequently in the midst of the sinus ; in the *Polyzoa*, the two orifices coalescing, the ganglion can no longer occupy the position it held in the *Tunicata* ; it is, therefore, carried backwards, and, still bathed in the fluid of the sinus, now becomes situated on the oesophagus, a difference of position which, it will easily be seen, involves no important change of relations, and which is necessarily connected with the difference in the arrangement of the other organs in the respective groups. In the *Polyzoa*, from their constant motions of retraction and exsertion, the ganglion could not occupy the fixed position which it does in the *Tunicata*, and, therefore, comes to be situated upon the polypide itself, all whose motions it then necessarily follows.

7. *Generative System.*—The construction of the generative system in the *Tunicata* and *Polyzoa* is also in conformity with the views of the present memoir. Both are hermaphrodite ; in both we have, besides true sexual generation, generation by gemmation, the gemma in the *Polyzoa* being formed exactly as in the *Tunicata* from a diverticulum of the sinus system.

Though our knowledge of the developmental phenomena is in many respects so deficient as to afford much less assistance in the present inquiry than could be desired, yet if we compare the embryological development of an Ascidian as given by MILNE-EDWARDS or VAN BENEDEK, with that of a Polyzoon, we shall still find the results in accordance with the views of the present paper. In the embryo-Ascidian, after the internal organs have begun to assume the definite form which is subsequently to characterize them, we find that the in-

terior of the body presents from behind forward four cavities, more or less distinguishable from each other, and which there is no difficulty in recognising as the future intestine, stomach, oesophagus, and respiratory sac. As yet, however, there is no trace of longitudinal or transverse bars in the respiratory sac, and it is only at a subsequent period that these bars come to line its walls. Observations are here deficient, but so far as they go it would seem that the transverse bars first make their appearance, that the longitudinal then show themselves; and lastly, that the sac becomes pierced by the respiratory stigmata. The circumstances under which the minute tentacula within the orifice of the respiratory sac become developed have not yet been satisfactorily observed. So many difficulties oppose themselves to our observation of the development of the *ovum* in the *Polyzoa*, that no facts of importance in the determination of the present question can thence be derived; but if we examine the corresponding development of the *bud* of *Paludicella*, we shall find after a time, that the nascent Polyzoon presents three distinct cavities, which are to become intestine, stomach, and oesophagus, and which are manifestly homologous with the cavities to which we give the same names in the embryo-Ascidian. Instead, however, of the closed cavity which in the Ascidian lies anterior to the oesophagus, and is to constitute the respiratory sac, we have here the anterior extremity of the oesophagus surrounded by a ring—the future lophophore—round whose outer margin a number of minute tubercles soon show themselves, and these then, becoming elongated, constitute the tentacula of the Polyzoon. Now between the formation of these tentacula and that of the respiratory bars of the *Ascidiae*, the resemblance appears quite complete; in *Paludicella* and most other *Polyzoa*, there is, it is true, nothing homologous with the proper membrane of the respiratory sac of the *Ascidiae* (the caliciform membrane of *Fredericella* and the hippocrepian *Polyzoa* being here absent), and consequently the closed *præbuccal* chamber of the *Ascidiae* does not exist in them; but the essential part of the respiratory apparatus—the transverse bars of the Ascidian and the tentacula of the Polyzoon—entirely correspond in their order and mode of development, and so far the evidence derived from the phenomena of development coincides with that afforded by anatomy. In *Fredericella* and the hippocrepian *Polyzoa*, the proper membrane of the sac shows itself in the form of a delicate calyx, which surrounds the base of the tentacular plume; the difficulty of observing the deve-

lopment of the bud through the more opaque tissues of these *Polyzoa* has rendered us here deficient in the class of facts now under discussion, and we are not, therefore, yet prepared to institute an actual comparison between the development of the branchial membrane in the *Ascidiae* and the caliciform membrane in the hippocrepian *Polyzoa*; so far, however, as our imperfect observations go, the facts are still in accordance with the views of the present paper; and though we have but little positive evidence to assist us in our conclusions, yet there is not a single observation tending to disprove the position that the branchial membrane of the one, and the caliciform membrane of the other, present in the circumstances of their development the conditions of homologous organs.

Among the other points of resemblance between the two groups, it is interesting to observe the frequent occurrence among the *Tunicata* of definite compound phytoidal forms resulting from gemmation, exactly as in the *Polyzoa*.

From what has now been stated it must be manifest, that the *Tunicata* and the *Polyzoa* are more nearly related to one another than either to any other branch of the animal kingdom; that they really belong to one and the same great structural type; and that the differences between them are non-essential modifications of this type, rendered for the most part necessary by the new power superadded upon the *Polyzoa* of alternately projecting and retracting the respiratory crown and anterior portion of the digestive organs through the external orifice of the cell.

The homology of the organs in the *Tunicata* and the *Polyzoa*, which it has been the object of the present paper to demonstrate, will be rendered more apparent by bringing together the equivalent organs of the two groups in the following two parallel series:

TUNICATA.	POLYZOA.
External tunic,	= Ectocyst.
Middle tunic,	= Endocyst.
Internal tunic,	= Tentacular sheath.
Sinus system,	= Perigastric space,
Respiratory orifice,	= External orifice of cell.
Cloacal orifice,	= Tentacula.
Transverse respiratory bars,	= Tentacula.

TUNICATA.	POLYZOA.
Branchial sinus,	= Lophophore.
Membrane of respiratory sac, =	Caliciform membrane.
Languet,	= Oral valve.
Cloaca,	= Space between tentacular crown and sheath.
Œsophagus,	= Œsophagus.
Stomach,	= Stomach.
Intestine,	= Intestine.
Muscles of middle tunic, .	= Parietal muscles.
Muscles of internal tunic (<i>Salpa, Dolioium</i>), . . .	= Sphincters of internal tunic.
Ganglion,	= Ganglion.
Tentacula,	= 0
Longitudinal respiratory bars, =	0
Heart,	= 0